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SIZE-STRUCTURED COMPETITION AND PREDATION IN RED-EYED
TREEFROG TADPOLES

A thesis submitted in partial fulfillment of the requirements for the degree of Master of
Science at Virginia Commonwealth University.

by

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Abstract

SIZE-STRUCTURED COMPETITION AND PREDATION IN RED-EYED TREEFROG TADPOLES

By Christopher Michael Asquith, Master of Science

A thesis submitted in partial fulfillment of the requirements for the degree of Master of
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Virginia Commonwealth University, 2010

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Body size is important in determining the outcome of competition and predator-prey interactions. Size structure of a population (i.e. relative proportion of large and small conspecifics) may be particularly important in organisms with prolonged breeding periods and rapid growth where populations may have multiple cohorts at different stages of development competing for one resource. Both the consumptive and nonconsumptive effects of predators can also be size-dependent and can alter competitive interactions. Here we study the importance of size structure in the Neotropical leaf-breeding tree frog, *Agalychnis callidryas*. This species is a prolonged breeder such that multiple overlapping cohorts of differing sizes are common. Specifically, we examine size-specific intraspecific competition between *A. callidryas* tadpoles and then explore how predation

affects these interactions. To determine the strength of inter-cohort competition, we manipulated the density and relative proportion of large and hatchling tadpoles in a response surface design and quantified growth. We then observed the effect of a dragonfly larvae predator (*Anax amazili*) on tadpole growth and survival at different size-structured treatments. Large tadpoles were greater per individual competitors while hatchlings were greater per gram competitors. When predators were added, dragonflies reduced survival and growth of hatchlings substantially, but had no effect on large tadpoles. Further, dragonflies reduced hatchling growth more when other hatchlings were present. The predator effect on hatchling growth was 23% larger than the effect of competition with large tadpoles, such that the importance of size structure for *A. callidryas* may be mediated more through predation than intercohort competition.

INTRODUCTION

Body size variation is common among individuals of many populations, and the structuring of populations with regard to size can play an important role in the growth and survival of individuals of different size classes. Differences in size among individuals can arise via inputs of new recruits into populations composed of older cohorts at later stages in ontogenetic development and may shape competitive (Werner 1994, Aljetlawli and Leonardsson 2002, Nishizaki and Ackerman 2004, Samhoury et al. 2009) and predator-prey interactions (Dixon and Baker 1988, Rodriguez 2009, Harter and Heck 2006, Sundell and Norrdahl 2002). Understanding how body size of individuals and the size structure of the population (i.e., relative proportion of large and small conspecifics) affect these ecological interactions might, therefore, be particularly important in organisms with prolonged breeding periods and multiple cohorts at different stages of development and growth. Because the size structure of these populations may vary greatly spatially or temporally, similar-sized individuals of different populations may thus experience different pressures depending on the size and abundance of conspecifics.

Body size is a major factor determining the symmetry, strength, and direction of competitive interactions (Kisdi 1999). These body size driven asymmetries likely result from different strategies and advantages afforded to individuals of different sizes (Persson 1985). Larger-bodied animals are better able to interfere with resource acquisition by smaller individuals through aggression or intimidation (Smith 1990). Smaller animals, however, have smaller energy budgets and can withstand a more marked reduction in resources under resource-limited circumstances (Persson 1985). Because the efficacy of these two mechanisms varies among species and environment, large or small individuals could be the dominant competitor for a given population (Persson and de Roos 2006). Regardless of which size class is the dominant competitor in the system, size structure in a population could affect growth rates of a population under resource-limited conditions.

Predators can also shape the growth and survivorship of prey populations through lethal, density-thinning effects and non-lethal, behavior-modifying effects, both of which are frequently size-dependent (Urban 2007, McCoy and Bolker 2008, Vonesh and Bolker 2006). Although large prey can be energetically more rewarding to predators, larger prey items can also be harder to capture or handle and consequently result in more frequent failed predation attempts (Nilsson and Bronmark 2000, Claessen et al. 2002). Thus, prey selectivity in predators is a function of both maximizing energy intake while minimizing energy spent on unsuccessful predation attempts (Micheli 1995). Individual prey, however, can often lower predation risk by reducing activities such as foraging that leave them vulnerable to predators (Preisser et al. 2005). These predator-induced behaviors increase survivorship, but are often adopted at the cost of reducing growth (Anholt and

Werner 1995).

Because competition and predation are not acting in isolation in natural systems, the interaction between the two processes can also shape growth and survivorship in prey populations. The presence of a predator can induce avoidance strategies that lower mortality risk but also incur costs to competitive abilities of the prey such as reduced growth and fecundity (Kerfoot 1997). Additionally, predators can alter competition through the disproportionate consumption of more vulnerable prey, leaving less vulnerable prey with greater resource availability as the density of competitors is thinned (Persson et al. 1996, Peacor and Werner 2001).

The red-eyed treefrog (*Agalychnis callidryas*) is a leaf-breeding hylid frog that is widespread throughout lowland tropical rainforests in Central America. Because these anurans breed continuously throughout the rainy season from May to November and larval period typically lasts from one to three months, new hatchlings must compete for resources with cohorts that arrived earlier in the season and have yet to emerge from the pond. As larvae, these tree frogs primarily consume suspended vegetation in the water column (Wassersug and Rossenberg 1979). A common predator of *A. callidryas* larvae in these breeding pools are larvae of the aeshnid dragonfly *Anax amazili*. Aeshnid larvae are only limited by gape constraints to large tadpoles, but have shown preference for smaller tadpoles in feeding trials (Brodie and Formanowicz 1983).

Here we evaluated how body size and population size structure shape growth and survivorship of two size classes of red-eyed tree frog tadpoles. Specifically, we determined the strength of intraspecific competition within and between tadpole size classes as well as how these interactions are altered in the presence of a lethal size-

limited predator. By independently manipulating competitor density and relative abundance, we quantified the reduction in growth of each size class resulting from intra- and intercohort competition. We predicted that larger tadpoles would have a stronger negative effect on tadpole growth, but that small tadpoles would be more resilient to growth depression than large tadpoles (Werner 1994). Further, when lethal predators are added to the system, both size classes should increase average growth due to greater per capita resources as a result of tadpole thinning. Finally, predator risk should be asymmetrical with regard to size with predators benefiting invulnerable large tadpoles by reducing the density of small tadpole competitors through consumption (Peacor and Werner 2001). These experiments provide insight into how the biotic pressures and the size structure context of a population can affect tadpole growth and predation risk.

MATERIALS AND METHODS

To test for intraspecific competition between size classes in *Agalychnis callidryas* tadpoles and how a lethal aquatic predator might influence this relationship, we conducted two mesocosm experiments at the Smithsonian Tropical Research Institute field station in Gamboa, Panama. These experiments were conducted during the rainy season in July and August of 2009. All *A. callidryas* larvae used in these experiments were reared from egg clutches collected from Experimental Pond, a man-made pond adjacent to forest.

Size-specific competition in *A. callidryas*

This experiment used a factorial design to measure the per capita and per biomass effect of large and hatchling tadpoles on tadpole growth rates. Hatchling tadpoles of three densities (2, 5, and 10 individuals) were crossed with large tadpoles of three densities (2, 5, and 10 individuals) in plastic containers, either round 60 L containers (44 cm diameter x 40 cm deep) or rectangular 40 L containers (28 cm tall x 25 cm wide x 58 cm long). All containers were filled with 35 L of mixed rainwater/aged tap water resulting in tadpole densities from 0.55 tadpoles L⁻¹ to 0.11 tadpoles L⁻¹ (natural larval densities of *A. callidryas* in Gamboa are found up to 0.16 tadpoles L⁻¹, Vonesh and Touchon, *unpubl.*). These nine treatments were randomized within five replicated blocks for a total of 45 containers (three blocks of round containers, two blocks of rectangular containers). Each container was given five large leaves for benthic covering

and covered by fine nylon mesh held in place with elastic bands to prevent colonization of non-experimental organisms.

Twelve newly laid egg clutches were collected on July 2 and manually induced to hatch at six days development, the natural peak of hatching for *A. callidryas* in Gamboa (Warkentin 2005), by submerging and lightly prodding embryos. Large tadpoles were obtained by adding hatchlings to 300 L cattle tanks and feeding them Spirulina and Sera[®] micron ad libitum until they reached a minimum size of 30 mm in length (~ 14 days). At the beginning of the experiment, hatchlings and large tadpoles averaged $11.13 \text{ mm} \pm 0.86$ and $37.16 \text{ mm} \pm 3.61$ total length (TL), respectively (mean \pm SD, here and throughout). On July 8, tadpoles were randomly assigned to treatments, digitally photographed, added to containers, and fed. Tadpoles were fed 0.1 g of Sera[®] micron per container initially and after four days (a limiting amount of resource based on McCoy et al. *unpubl.*). Within size classes, initial TL for hatchlings ($F = 0.89$, $P = 0.53$) and large tadpoles ($F = 0.29$, $P = 0.97$) were not significantly different between treatments.

On July 17 tadpoles were removed from the experiment, digitally photographed, and measured using image analysis software ImageJ (<http://rsb.info.nih.gov/ij/>) to estimate growth. To noninvasively estimate mass for each tadpole, a mass to total length regression curve from field data (Vonesh *unpubl.*, $y = 0.00005x^{2.9}$, $r^2 = 0.99$) was used. Hatchlings were estimated to be $0.010 \text{ g} \pm 0.002$ and large tadpoles were estimated to be $0.328 \text{ g} \pm 0.090$, respectively.

Predator effects on size-structured *A. callidryas* populations

To examine size specific differences in mortality and growth as driven by a lethal aquatic predator and the size structure of the tadpole population, we conducted a 2 x 3

factorial randomized block design with two predator treatments (presence and absence) and three size structure treatments (20 large tadpoles alone, 20 hatchlings alone, or 10 large tadpoles/10 hatchlings). These six treatments were replicated five times in 300L tanks (N = 30 tanks total). Each tank was given 50 g of leaf litter for benthic cover and covered with fiberglass screen (mesh diameter 1.2 mm) and held down with rubber tubing to prevent colonization of non-experimental organisms.

Twenty newly oviposited clutches were collected on July 21, hatched after six days, and maintained for two days in 40L plastic containers. Large tadpoles were obtained as above. Initially, hatchlings and large tadpoles were on average $14.10 \text{ mm} \pm 1.29$ and $38.13 \text{ mm} \pm 3.27$ TL, respectively. Within size classes, initial TL was not significantly different among treatments for hatchling ($F = 0.25$, $P = 0.86$) or large tadpoles ($F = 0.08$, $P = 0.97$). Dragonfly larvae of the Amazon darner (*Anax amazili*) were used as aquatic predators and were captured by dipnetting from Quarry Pond on July 28. Dragonfly larvae were 31.27 ± 3.61 mm and maintained individually in water-filled cups without food for about 24 hours prior to the experiment.

Dragonfly larvae and tadpoles were randomly assigned to predator treatments, digitally photographed, added to tanks, and fed 0.3 g Sera micron on July 29. On August 3, tadpoles were fed in the same manner and dragonfly larvae were removed from the tanks. Tadpoles were removed the following day and digitally photographed and measured as above.

Statistical Analyses:

We tested for effects of additional hatchling and large tadpoles at different densities and size structures on the growth and survival of total tadpoles, large tadpoles, and

hatchlings using a mixed-effects generalized linear model (GLM). These analyses were performed using hatchling and large tadpole density and biomass as factors. Parameters for effects of tadpole density and biomass on tadpole growth and survivorship were estimated using mixed-effects GLMs with Gaussian family, logit link, and spatial block as the random factor. We used likelihood ratio Chi-square tests assuming binomial distributions to test the effects of tadpole density and biomass on survivorship and two-way factorial ANOVAs to test the effect of large and hatchling tadpoles on tadpole growth.

For the predation experiment, we used mixed-effects GLMs to determine the effect of predators and population size structure on total, hatchling, and large tadpole growth and survivorship. Likelihood ratio Chi-square tests and two-way factorial ANOVAs were used as above with predator and size structure treatments as factors to test their effect on survivorship and growth, respectively.

Random block effects were non-significant and removed from all analyses. Interactions in models were only retained if significant. Normality assumptions for parametric tests were verified using Shapiro-Wilks tests, and homoscedasticity was assessed using Bartlett's tests. Total tadpole, large tadpole, and hatchling growth in the competition experiment were natural log transformed, and for large tadpole growth in the predation experiment we used a squaring transformation to normalize a naturally left skewed distribution. All statistical analysis was performed using R version 2.10.1 (R Development Core Team 2009).

RESULTS

Competition Experiment:

Density effect: Mean larval growth of both size classes was more reduced by increasing large tadpole density than hatchling density. Hatchling tadpole growth was significantly reduced by large tadpole density ($F_{1,41} = 82$, $P < 0.0001$) and hatchling density ($F_{1,41} = 7.0$, $P = 0.01$). Hatchling growth declined at a rate of 0.20 mg d⁻¹ per hatchling (Linear Model, $t = -2.6$, $P < 0.0001$, Table 1) and 0.40 mg d⁻¹ per large tadpole ($t = -9.1$, $P < 0.0001$). Large tadpole growth was significantly reduced by large tadpole density ($F_{1,41} = 77$, $P < 0.0001$), but not hatchling density ($F_{1,41} = 1.6$, $P = 0.21$). Large tadpole growth decreased by 1.05 mg d⁻¹ per large tadpole ($t = -8.8$, $P < 0.0001$) and trended toward a decrease of 0.80 mg d⁻¹ per hatchling ($t = -1.3$, $P = 0.21$). There was no interaction between hatchling and large density for hatchling growth ($F_{1,41} = 1.5$, $P = 0.23$) or large tadpole growth ($F_{1,41} = 0.64$, $P = 0.43$).

Biomass effect: While large tadpole density decreased tadpole growth in both size classes more than hatchling density, hatchling biomass had a greater effect on the growth of both size classes than large tadpole biomass. Hatchling tadpole growth was significantly reduced by large biomass ($F_{1,41} = 83$, $P < 0.0001$; Fig 1a.) and hatchling biomass ($F_{1,41} = 7.2$, $P = 0.01$). Hatchling growth decreased by 0.18 mg d⁻¹ per 0.01 g hatchling biomass ($t = -2.7$, $P = 0.01$) and 0.011 mg d⁻¹ per 0.01 g large tadpole biomass ($t = -9.2$, $P < 0.0001$; Table 1). Large tadpole growth was significantly reduced by large tadpole

biomass ($F_{1,41} = 85$, $P < 0.0001$; Fig 1b.), but not hatchling biomass ($F_{1,41} = 2.5$, $P = 0.12$). Large tadpole growth decreased by 0.03 mg d⁻¹ per 0.01 g large tadpole biomass ($t = -9.3$, $P < 0.0001$) and trended toward decreasing by 0.84 mg d⁻¹ per 0.01 g hatchling biomass ($t = -1.6$, $P = 0.12$). There was no interaction between hatchling and large tadpole biomass on hatchling growth ($F_{1,41} = 0.23$, $P = 0.63$) or large tadpole growth ($F_{1,41} = 0.60$, $P = 0.44$). Tadpole survivorship was high (proportion surviving = 0.97) and not affected by large tadpole biomass (Likelihood Ratio χ^2 , $\chi^2 = 0.054$, $P = 0.82$) or hatchling biomass ($\chi^2 = 0.18$, $P = 0.67$).

Predation Experiment

The presence of predatory dragonfly larvae significantly reduced overall tadpole survival ($\chi^2 = 15$, $P < 0.0001$), and hatchlings were significantly more vulnerable than large tadpoles ($\chi^2 = 4.7$, $P = 0.03$). Predators did not alter large tadpole survival ($\chi^2 = 1.34$, $P = 0.25$; Fig 2a), although it appears there was some predator-attributed mortality (31% \pm 23% SD with predators, 8% \pm 12% SD without predators) and thus large tadpoles may not have been completely invulnerable. Dragonflies reduced hatchling survivorship 81% ($\chi^2 = 16$, $P < 0.0001$; Fig 2b). Cohort structure did not affect overall tadpole survival ($\chi^2 = 0.013$, $P = 0.91$) and did not alter the effects of a predator on hatchling ($\chi^2 = 0.17$, $P = 0.68$) or large tadpole survivorship ($\chi^2 = 0.27$, $P = 0.60$).

For large tadpoles neither the predator treatments ($F_{1,13} = 0.15$, $P = 0.71$; Fig 3a.) nor cohort size structure ($F_{1,13} = 1.0$, $P = 0.33$) altered growth. Despite the large consumption effects of dragonflies on hatchlings, the presence of predators reduced hatchling growth by 63% ($F_{1,13} = 91$, $P < 0.0001$ Fig 3b.). Similarly, hatchlings grew significantly less in the presence of large tadpoles compared to when reared with other hatchlings ($F_{1,13} = 35$,

$P < 0.0001$). For hatchlings, the predator by size structure interaction was also significant, with predators reducing growth more markedly when only hatchlings were present ($F_{1,13} = 6.3$, $P = 0.026$).

DISCUSSION

Our results highlight the importance of body size and size structure context for shaping intra- and interspecific interactions within red-eyed tree frog tadpoles. Competition was size dependent with large tadpoles as greater per individual and hatchlings as greater per gram competitors. However, competition was not dependent on size structure. When present, dragonfly predators reduced survival and growth of hatchlings substantially, but had no effect on large tadpoles. For hatchling tadpoles, predators altered competition such that hatchling growth was higher when competing with other hatchlings instead of large tadpoles. Nonlethal predator effects also reduced hatchling growth 23% more than the effect of competition with large tadpoles, potentially nullifying the importance of competition when dragonflies are present.

For tadpole competition in the absence of a predator, we find that the competitive effects of large tadpoles and hatchlings are asymmetric, with large tadpoles having stronger per capita effects than hatchlings on growth rates of both hatchlings and other large tadpoles. We found the addition of one large tadpole would have twice the effect on hatchling growth and a 30% greater effect on large growth than the addition of one hatchling. This advantage could be due to differences in traits, such as large tadpoles having a larger filtering surface and thus removing resources at a faster rate than small tadpoles, or behavioral in nature (e.g., reducing hatchling growth through intimidation). However, from a per unit biomass perspective, hatchling tadpoles had a far greater effect on growth reduction of both tadpole size classes. In our experimental venues the addition

of 1 gram of hatchlings would reduce hatchling growth 16 times more and large tadpoles about 28 times more than the addition of 1 gram of large tadpoles. This per unit biomass advantage is likely due to the lower cost of maintaining hatchling energy budgets and the higher net gain for smaller organisms consuming an equivalent amount of resources as larger individuals.

Werner (1994) compared effects of competitive interactions between size classes of two species of larval anurans to hypothetical cost and gain curves appropriate for larval anurans. Our results support his findings that because gain curves scale to body size monotonically, large tadpoles should be better per capita competitors, with energy consumption increasing with mass. Furthermore, because these gain curves decelerate as an individual's size increases, small tadpoles can consume a fixed quantity of resources more efficiently than a group of large tadpoles of equivalent biomass. Our experiment varies tadpole densities as well as relative proportion for both size classes allowing us to quantify the effect of the impact that the addition of an *A. callidryas* larva has on the growth of the tadpoles of both size classes under conditions of limited resources.

The asymmetries in competition likely arise from both differing size-dependent rates of filtration as well as size-dependent resource utilization. Our model for tadpole growth as a function of competitor densities supports the conclusion that large tadpoles are better able to reduce the growth of competitors, as the effects for large tadpoles on other large tadpoles and hatchlings were higher than hatchling tadpole density on either size class. However, hatchling tadpole growth was reduced relatively less by competitors of either size class than large tadpoles. This competitive ability to withstand reductions in growth better than larger-bodied tadpoles may provide long-term advantages for hatchlings

should resources in the aquatic environment become limiting. In natural ponds, hatchlings may use this advantage to survive until larger cohorts undergo metamorphosis and are no longer competitors, allowing the next cohort of tadpoles to dominate resources before emerging from the pond. Reduced growth at the larval stage, however, can prolong this vulnerable ontogenetic period and reduce size at metamorphosis. Several studies have provided evidence that a smaller size at metamorphosis can lead to long-term costs in fitness for many organisms with complex life cycles (Chelgren et al. 2006, Hentschel and Emlet 2000, De Block and Stoks 2008).

When predators were added to the system, predator effects were strongly dependent with regard to size. Hatchling growth and survivorship were dramatically affected by *A. amazili* consumptive and nonlethal effects while large tadpole growth and survivorship were not significantly different between treatments. The influence of nonlethal predator effects on hatchling growth is evident from the greater decline in hatchling tadpole growth in lethal predator treatments despite an increase in per capita resources due to the thinning of 85% of hatchlings. This reduction in growth is likely due to a phenotypic response in behavior in which foraging time is sacrificed in favor of predator avoidance strategies (Van Buskirk et al. 1997). Absolute growth in hatchlings was further reduced in a non-additive manner when large tadpoles were included in treatments, demonstrating that hatchlings were still limited to the available resources even at reduced foraging rates.

Werner and Anholt (1996) found similar results in a temperate, multiple-species system using a different *Anax* species as the predator and larvae of two ranid frog species of different sizes as the competitors. Similar to our study, Werner and Anholt (1996) found that nonlethal dragonfly predators significantly reduced small tadpole growth.

However, our findings differ in that nonlethal predators increased large hatchling growth in their experiment while our large tadpole growth was unaffected by predator presence. One important distinction between our designs, however, is that large tadpoles in Werner and Anholt's predation study were of a size invulnerable to predation, whereas our large tadpoles experienced some mortality, although not significantly. Though *Anax* predators altered the strength (and in some cases direction) of competition in both temperate and tropical system experiments, predators had much stronger impact on small tadpole growth in our experiment. In fact, the presence of lethal predators reduced hatchling growth by 64% on average, while the effect of substituting half of the hatchlings with large tadpoles reduced hatchling growth by about 41%. With actual predator densities in nature potentially ranging much higher than was experimentally manipulated (Vonesh and Touchon, *unpubl.*), predators could have a much larger role in tadpole growth than competitors of any size class.

In addition to the large, size-dependent effect of predators on hatchling growth, the size structure of the population also impacted hatchling growth. Hatchlings grew less in mixed cohort treatments than amongst other hatchlings, similar to hatchling growth observed in the competition experiment. Interestingly, the effect of predators on hatchling growth was size structure dependent, with predators having a greater effect on hatchling growth in the absence of large competitors. This larger reduction in hatchling growth may be due to the higher mortality in the hatchling single cohort treatments where more predator chemical cue was likely in the water (Fraker 2009).

The proportion of large tadpoles surviving decreased on average from 97% in non-predator tanks to 69% in treatments with lethal predators, indicating that large tadpoles

were somewhat vulnerable to *A. anazili* larvae, even if this difference was not statistically detectable. Large tadpoles, however, are likely more satiating or more energetically expensive to capture, and consequently were not consumed at the same rate as hatchling tadpoles. This result could also be due to the “size refugia” concept, where organisms that have reached a less-vulnerable size from a gape-limited predator will have different predator avoidance strategies than more vulnerable prey (Tejedo 1993, Urban 2007) or because the duration of the experiment was not adequate to accurately determine risk to large tadpoles. Growth for large tadpoles was unaffected by *A. amazili* presence, and, though not significant, growth rates tended to be higher in treatments with only large tadpoles and predators compared to treatments of only large tadpoles and no predator. Since predators do not significantly affect large tadpole mortality, large tadpoles would not benefit from costly predator avoidance behavior and thus do not react to nonlethal effects of dragonflies by reducing growth. Consequently, large tadpole growth appears to be largely driven by resource availability as opposed to predator effects.

Our results highlight the importance of size and size structure in understanding competition and predation in systems with considerable size variation. Because of the asymmetrical nature of most competitive interactions in natural systems, individual size can be crucial in understanding the effects of inter-cohort competition. Additionally, predator effects can be size and size structure dependent as well as greater than competitive effects. In our system, we expected predation to decrease competition and increase growth by reducing the density of competitors. This pattern was absent in large tadpoles, most likely due to low predator-attributed mortality for large tadpoles. Conversely, the resulting net effect of both the lethal and nonlethal effects of predators on

hatchling tadpoles reduced hatchling growth. This reduction in hatchling growth with increased predation risk in spite of an increase in per capita resources is presumably due to a phenotypic, non-consumptive effect on hatchlings such as a reduction in activity level or foraging behavior. We have shown that these predator effects on growth can be stronger and potentially more important than effects from top competitors in populations. The inclusion of size-structure as well as predator effects is crucial to our understanding of population dynamics in which individual size is highly variable and predators are the most important factor in determining the growth of a subset of the population.

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Table 1. Reduction of average growth in mg d⁻¹ of target size classes with the addition of competitor size class individuals or biomass.

Target class	Competitor class			
	Large		Hatchling	
	per 0.01 g	per individual	per 0.01 g	per individual
Hatchling	-0.011 **	-0.40 **	-0.18 **	-0.20 **
Large	-0.03 **	-0.1.05 **	-0.84 NS	-0.80 NS

Figure 1. Figure 1: Mean growth of *Agalychnis callidryas* hatchling tadpoles (a) and large tadpoles (b) as a function of hatchling biomass in the competition experiment. Filled circles represent low biomass of large tadpoles (0.64 ± 0.04 g), open circles represent intermediate biomass of large tadpoles (1.62 ± 0.06 g), and filled triangles represent high large tadpole biomass (3.32 ± 0.08 g). The regressions represent the effect on hatchling growth as hatchling biomass is added and large tadpole biomass is held constant.

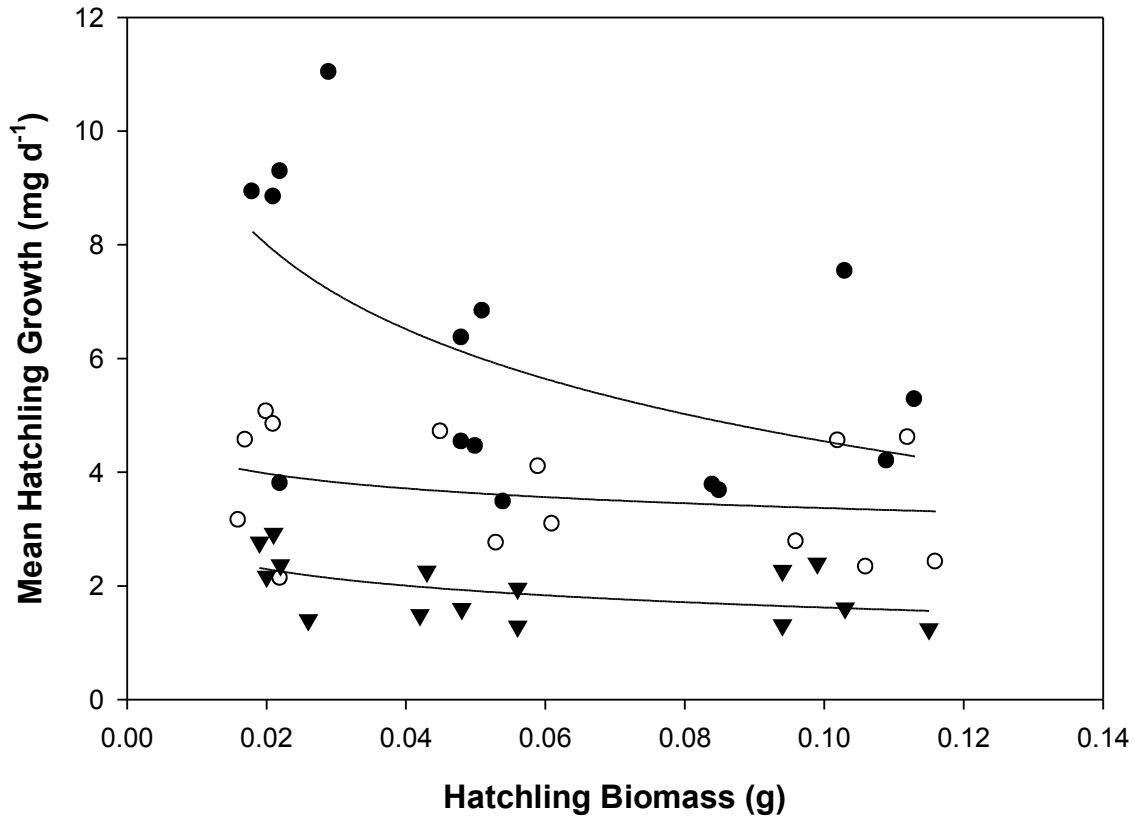


Fig. 1a.

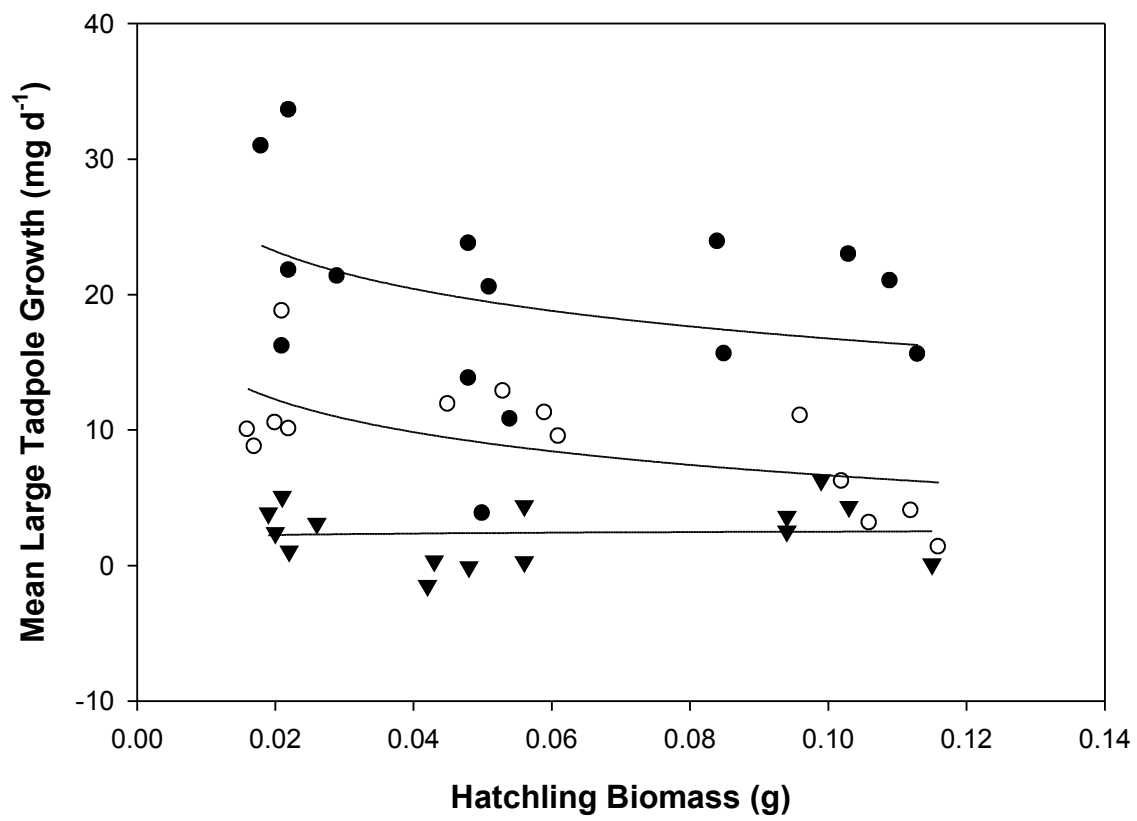


Fig 1b.

Figure 2. Effect of predator and size structure treatments on large (a) and hatchling (b) tadpole mean proportional survival. Filled circles represent mixed cohort treatments and open circles represent single cohort treatments.

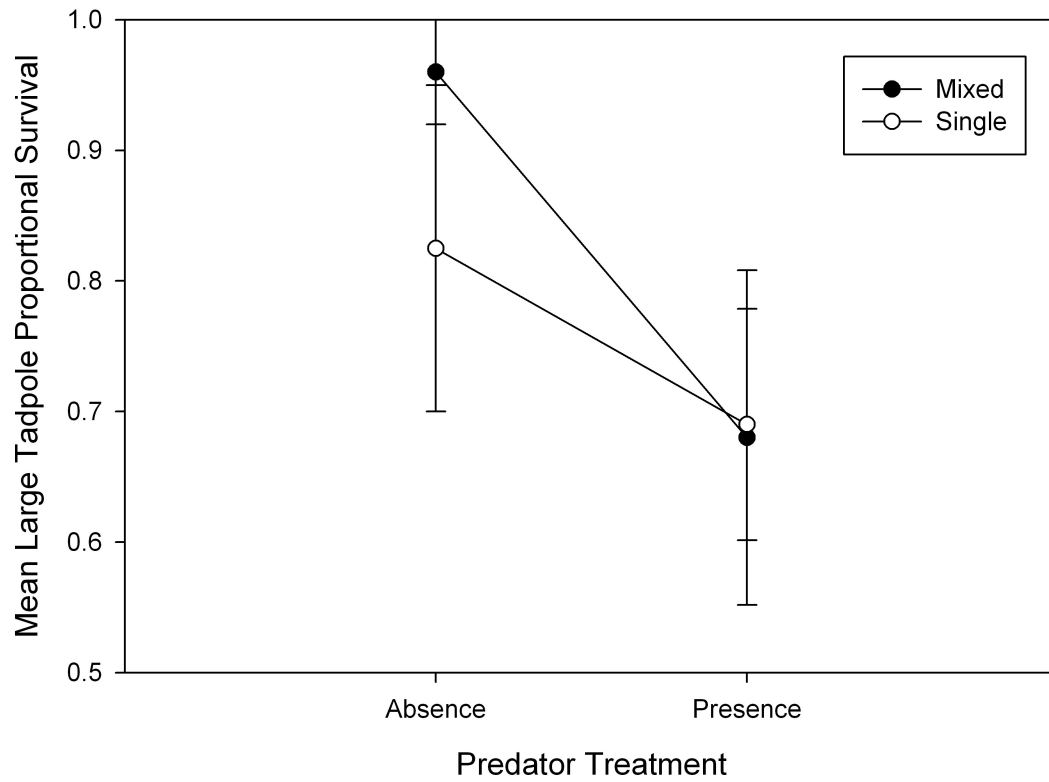


Fig 2a.

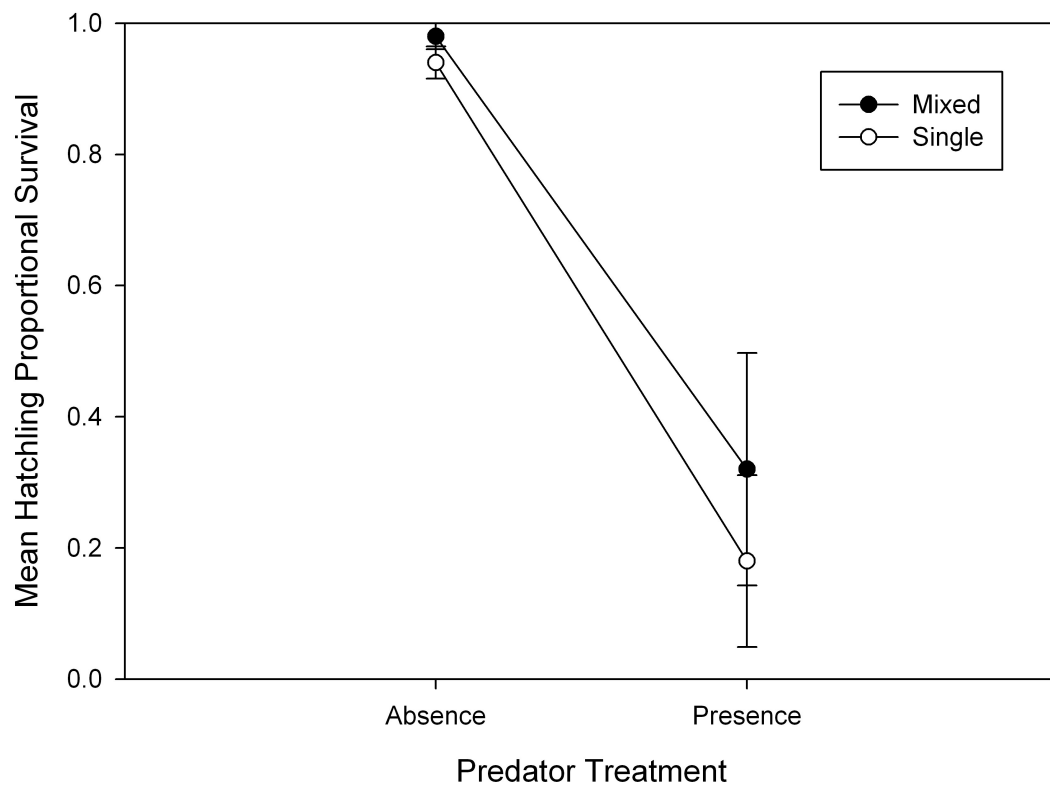


Fig 2b.

Figure 3. Effect of predator and size structure treatments on large (a) and hatchling (b) tadpole mean growth (mg d^{-1}). Filled circles represent mixed cohort treatments and open circles represent single cohort treatments.

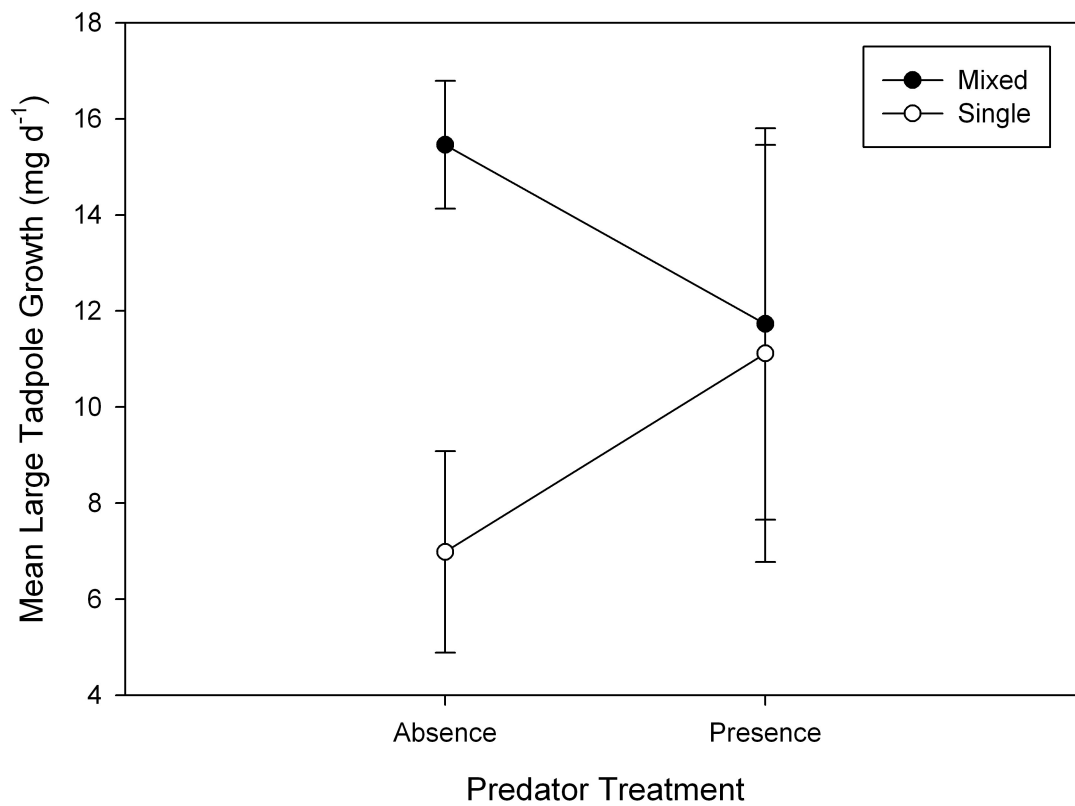


Fig 3a.

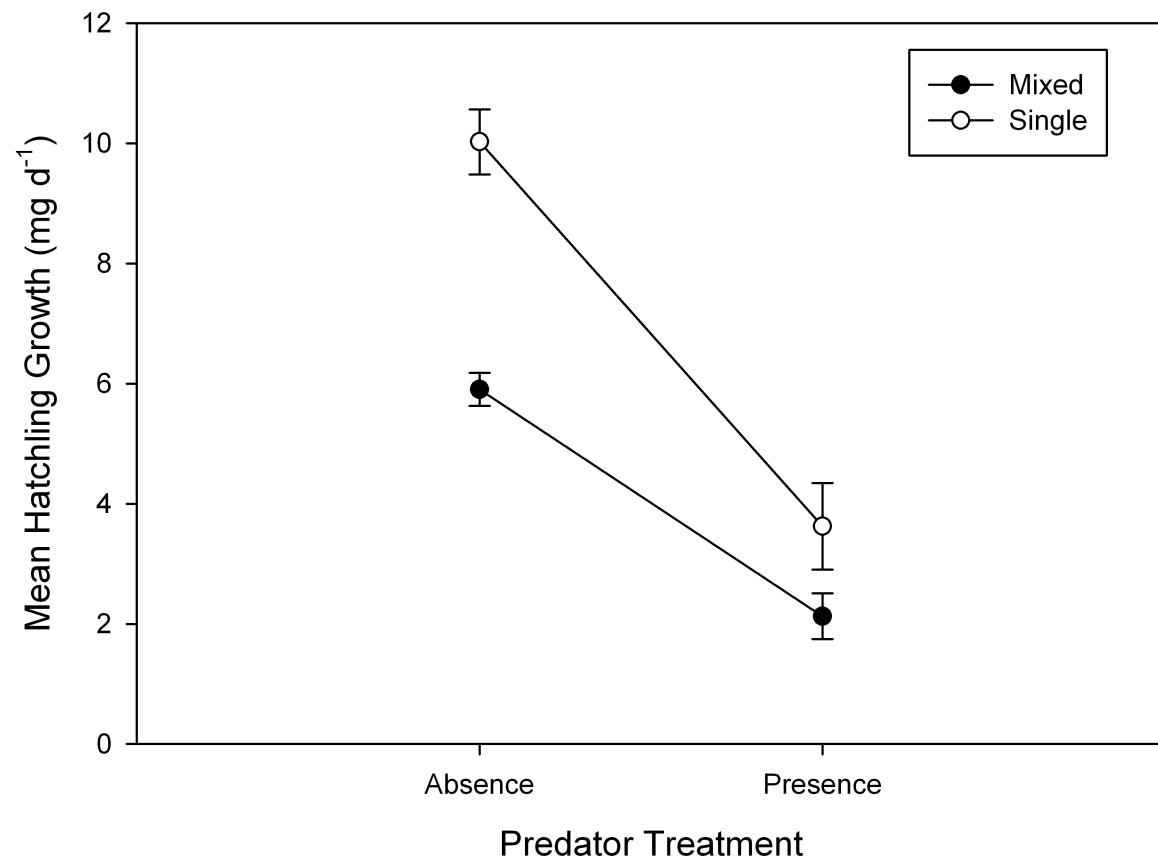


Fig. 3b.

Vita

Christopher Michael Asquith was born December 10, 1985 in Knoxville, Tennessee. He attended South-Doyle High School in Knox County, Tennessee and graduated second in his class in 2004. He attended Maryville College in Maryville, Tennessee and received a Bachelor of Arts in Biology with minors in Statistics and Chemistry, graduating Magna Cum Laude in 2004. He taught introductory level biology labs as a teaching assistant for two years while pursuing graduate studies at Virginia Commonwealth University. He received his Master of Science in Biology and Certificate in Geographic Information Systems from Virginia Commonwealth University in 2010.